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The tadpole of *Ptychadena aequiplicata* (Werner, 1898) with the description of a new reproductive mode for the genus (Amphibia, Anura, Ranidae)

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We describe the tadpole of *Ptychadena aequiplicata* (Werner, 1898) based on specimens from Taï National Park, Ivory Coast. Compared to other tadpoles of the genus it is unique by its bicoloured body, posterior part lighter than anterior one. *Ptychadena aequiplicata* is restricted to closed forest habitats. It has a reproductive behaviour unique to the genus. Clutches of numerous females were communally deposited on the forest floor, between leaves and small plants. Spawning sites were always situated at the edges of dried up ponds. Pre-hatching time was variable. Tadpoles still hatched two weeks after oviposition. In some specimens development continued in the large eggs up to Gosner stage 28. Developmental time from hatching to metamorphosis was less than two weeks. We regard this developmental mode as an adaptation to the surprisingly high desiccation risks of the forest ponds in Taï National Park.

INTRODUCTION

Ptychadena aequiplicata (Werner, 1898) is widespread in West and Central Africa (tab. 1). In its whole range it inhabits exclusively forest habitats (GUIBÉ & LAMOTTE, 1958; LAMOTTE, 1966; AMIET, 1974, 1975; LARGEN & DOWSETT-LEMAIRE, 1991), mainly primary rain forest (RIVA, 1994; BÖHME, 1994). While tadpole descriptions (GUIBÉ & LAMOTTE, 1958; LAMOTTE & ZUBER-VOGELI, 1953; LAMOTTE et al., 1958, 1959; LAMOTTE & PERRET, 1961; RÖDEL, 2000*a*) and biological data (BARBAULT & TREFAUT RODRIGUES, 1978; RÖDEL, 2000*a*) of many other

Table 1. – Known distribution of *Ptychadena aequiplicata*.

Country	Source
Guinea	BÖHME, 1994
Liberia	GUIBÉ & LAMOTTE, 1957, 1958; SCHIØTZ, 1968; EUZET et al., 1969
Ivory Coast	EUZET et al., 1969; LAMOTTE, 1967; RÖDEL, 2000*b*; this paper
Ghana	SCHIØTZ, 1964*a*
Nigeria	SCHIØTZ, 1963
Cameroon	PERRET, 1966; AMIET, 1974, 1975; LAWSON, 1993; FRETEY & BLANC, 2000
Central African Republic	FRETEY & BLANC, 2000
Republic of Congo	FRETEY & BLANC, 2000
Congo	LARGEN & DOWSETT-LEMAIRE, 1991; FRETEY & BLANC, 2000
Equatorial Guinea	RIVA, 1994; FRETEY & BLANC, 2000
Gaboon	FRETEY & BLANC, 2000

West African *Ptychadena* species are available, nearly nothing is know about the biology of this common forest frog. Its voice was made known by SCHIØTZ (1964*a*) and AMIET (1974). In all *Ptychadena* species where reproduction is known, spawn is deposited as a surface layer in stagnant waters of variable size (WAGER, 1986; RÖDEL, 2000*a*). In Taï National Park (TNP), Ivory Coast, we were able to identify *P. aequiplicata* tadpoles in 1999. Those tadpoles have been collected in forest ponds and raised to metamorphosis to assure species affiliation. However, other details of the frog's reproductive biology, especially spawning sites and clutches, remained unknown. In 2000 we found *P. aequiplicata* clutches deposited terrestrially at the edges of dried up forest ponds.

MATERIALS AND METHODS

STUDY AREA AND FIELD DATA

The TNP is the largest protected area of rain forest in West Africa. Our main investigation area was located 23 km southeast of the small town of Taï and comprises about 30 km^2 of primary and secondary rain forest around the Station de Recherche en Ecologie Tropicale (SRET; 5°50'N, 7°20'W). Between 1991 and 1999, mean annual precipitation at the SRET was 1,854 mm (*sd* 249; range 1,424-2,194 mm; R. Noë, pers. comm.). Most precipitation occurred from April to July and from September to November. The first dry period lasted from December to February, normally a second one occurred in August. The mean annual temperature was about 25°C. More detailed descriptions of the TNP are provided by GUILLAUMET (1967) and RIEZEBOS et al. (1994).

Data were collected irregularly in different parts of the forest, and regularly along 10 transects, 600 m in length. Six transects have been set up in primary and four in secondary forest. Data collection and transect conception were described in more detail in RÖDEL (2000*b*) and RÖDEL et al. (in press *a*).

PRESERVATION AND DESCRIPTIVE METHODS

Frogs were sacrificed in a chlorbutole solution and preserved in 4 % formaldehyde or 70 % ethanol. Later on all adults were transferred into ethanol. Larvae of different stages were preserved in 4 % formaldehyde. Measurements were taken with a dial calliper (± 0.1 mm) or a measuring ocular in a dissecting microscope (± 0.1 mm; Zeiss Stemi SV 6). We measured body length (BL), body width (BW, measured at the plane of the eyes), tail length (TL), fin height (TF), height of tail axis (TA) and body height (BH). Measures are given in mean values with standard deviation. Nomenclature of morphological features follows VAN DIJK (1966), ALTIG & JOHNSTON (1989) and ALTIG & MCDIARMID (1999). The labial tooth row formula is according to DUBOIS (1995). Staging of tadpoles was according to GOSNER (1960). The tadpole description is a summary of all specimens from Gosner stages 27-38. The description of the coloration is based on living tadpoles. Drawings were done with the aid of a camera lucida. Voucher specimens are deposited in the collection of the Staatliches Museum für Naturkunde Stuttgart (SMNS 9774.1-6, 2 males, 4 females; 9775.1-15, tadpoles; 9776.1-73, tadpoles).

REARING

Tadpoles were reared in plastic aquaria (PT2 Firma Hoch, 25 × 15 cm, 16 cm water depth), filled with rain water and fed ad libitum with commercial fish food (TetraMin®). Water was changed every day. As development in nature seems to be much faster (see below), we don't give any developmental time tables. Species affiliation was assured by tadpoles captured in forest ponds and partly raised to metamorphosis in 1999 (SMNS 9775.1-15).

RESULTS

TADPOLE DESCRIPTION

Body ovoid in dorsal view (fig. 1b); in lateral view slightly pointed (fig. 1a); body length 1.70 ± 0.08 (n = 51) times body width (measured at the plane of the eyes); body length 0.61 ± 0.05 (n = 51) tail length; eyes laterally; nostrils dorsolaterally, closer to snout tip than to anterior corner of the eyes; tail straight, if extrapolated, axis of tail passing through eyes; fin height nearly equal to body height (0.80 ± 0.08, n = 51); dorsal fin originating anterior to tail-body junction; dorsal and ventral fin nearly parallel to tail axis; tail tip rounded; small oral disc anteroventral, bordered by two to three rows of papillae with large rostral gap, caudal with few larger papillae; many additional papillae grouped in oral angles; jaw sheaths massive and serrated; upper jaw sheath evenly broad U-shaped; lower jaw sheath V-shaped; labial tooth row formula of tadpoles, older than stage 28, 1:2+2/2 or 1:2+2/1+1:1 (fig. 2; formulae of all stages are summarized in tab. 2); spiracle sinistral, visible dorsally;

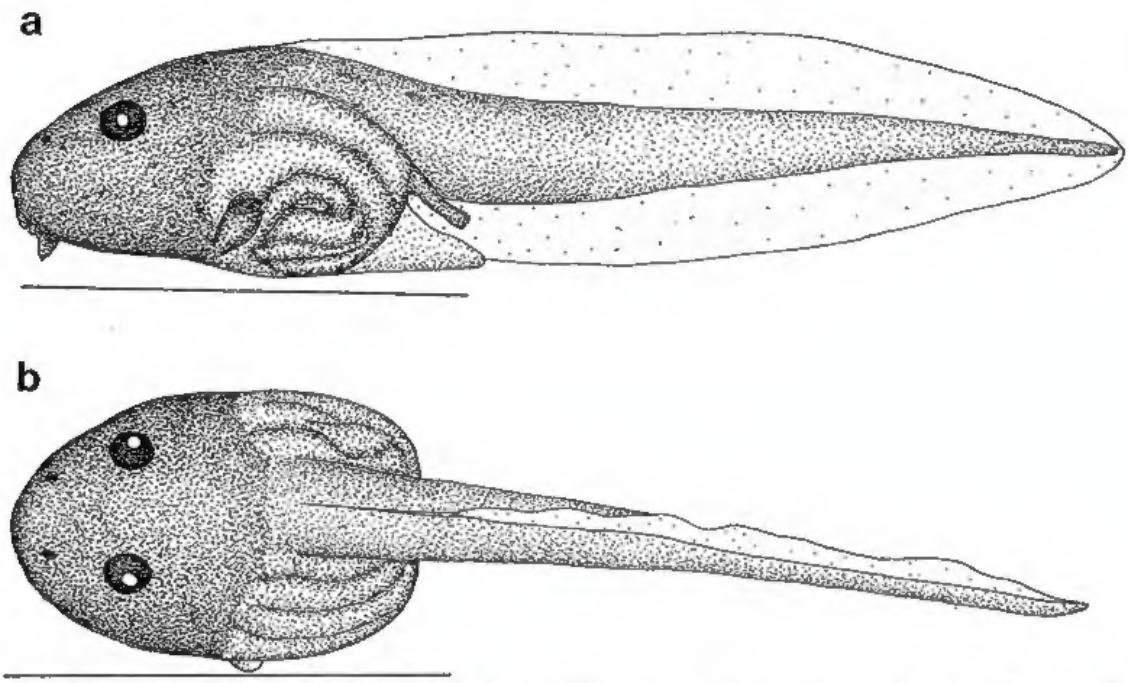

Fig. 1. – Lateral (a) and dorsal (b) view of a *Ptychadena aequiplicata* tadpole (stage 33) from Taï National Park, Ivory Coast. Scale bar: 10 mm.

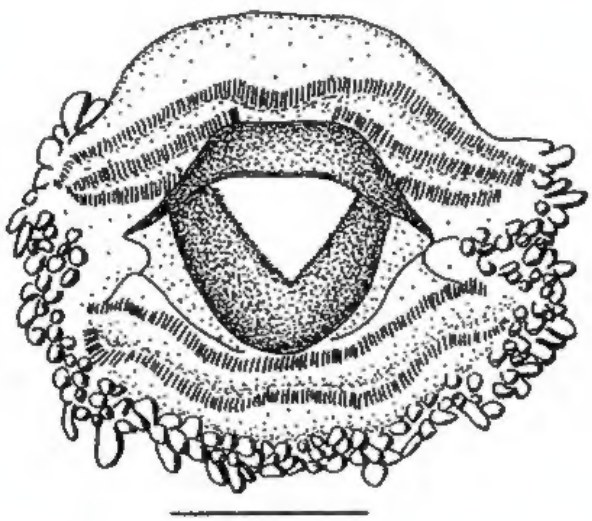

Fig. 2. – Oral disc of the specimen illustrated in fig. 1. Scale bar: 1 mm.

Table 2. – Labial tooth row formulae of *Ptychadena aequiplicata* tadpoles, sample size in parentheses. Stage after GOSNER (1960).

Stage	Labial tooth row formulae	Stage	Labial tooth row formulae
20	Not present (1)	31	1:2+2/1+1:1 (3); 1:2+2/2 (3)
22	Not present (1)	32	1:2+2/1+1:1 (4)
24	1/1+1:1 (1); 1:1+1/1+1:1 (4)	33	1:2+2/2 (2)
25	1/1+1:1 (6); 1:1+1/1+1:1 (3)	34	1:2+2/1+1:1 (3)
27	1:1+1/2 (1); 1:2+2/2 (1)	35	1:2+2/1+1:1 (1)
28	1:1+1/2 (4); 1:1+1/1+1:1 (3);	36	1:2+2/1+1:1 (6)
	1:2+2/1+1:1 (3); 1:2+2/2 (6)	37	1:2+2/1+1:1 (7)
29	1:2+2/2 (3)	38	1:2+2/1+1:1 (1)

vent opening medially, positioned basicaudally. Further measurements are summarized in tab. 3.

In life the tadpoles are bicoloured. The anterior part of the body is dark beige to brown, the posterior part is light brown to yellow. The tail axis becomes lighter towards the tail tip. The fin is transparent. The venter is slightly lighter than the back.

BIOLOGY

In *P. aequiplicata* sexes differ considerably in size. Mean size in females was 48.3 mm (range 39-64, $n = 8$), in males mean SVL was 39.5 mm (range 36-43, $n = 6$). Two dissected females (SMNS 9774.5-6; 58 and 54 mm SVL) bore 457 and 478 ovarian eggs, respectively. The eggs had a diameter of about one mm, and black and white poles.

Male's choruses were regularly heard after heavy rainfall throughout the whole rainy season. Calling males were always concealed between leaves or roots, several meters apart from filled or dried up forest ponds. Calling activity was mainly during night, rarely during day. Adults were registered in swampy areas, as well as in relatively dry parts of the forest without open water. Compared to other leaf-litter frogs, *P. aequiplicata* was not very abundant. We found 0.15 *P. aequiplicata* per transect hour in primary forest (289 h). During 93 transect hours in secondary forest we found only one *P. aequiplicata*. Tadpoles were continuously encountered throughout the rainy season. We found them only in stagnant forest ponds within primary rain forest. Juveniles were registered between end of June and beginning of November. They measured 14.8 ± 2.8 mm SVL (11-20 mm, $n = 31$).

At 2 p.m. on September 8th, we heard a large chorus at a dry pond after rainfall (site 1). While approaching the spot, about 50 *P. aequiplicata* jumped away (J. Fahr, pers. comm.). On September 15th, we discovered more than 2000 eggs at this site. The eggs were deposited on the ground between the stalks of herbs. The eggs were congregated on two areas, measuring 1.5 m^2 and 2 m^2, respectively. On September 18th, we found similar spawning sites at four other

Table 3. – *Ptychadena aequiplicata* tadpole measurements (mean ± standard deviation). Only tadpoles for which all measurements were available were taken into consideration. For abbreviations see *Materials and methods*. Stage after GOSNER (1960).

Stage	*n*	BL	BH	BW	TL	TF	TA	BL+TL	BL/BW	BL/TL	BH/TF
20	1	2.6	1.3	1.3	3.6	1.4	0.5	6.2	2.0	0.7	0.9
22	2	2.6 ± 0.1	1.2 ± 0.1	1.3 ± 0	3.6 ± 0.2	1.4 ± 0.1	0.5 ± 0	6.1 ± 0.3	2.0 ± 0.1	0.7 ± 0	0.9 ± 0
24	5	3.4 ± 0.3	1.5 ± 0.2	2.0 ± 0.3	5.6 ± 1	1.8 ± 0.3	0.8 ± 0.3	9.0 ± 1.3	1.7 ± 0.1	0.6 ± 0.1	0.9 ± 0.2
25	9	3.2 ± 0.2	1.5 ± 0.2	1.9 ± 0.2	5.2 ± 0.4	1.7 ± 0.3	0.8 ± 0.4	8.4 ± 0.6	1.7 ± 0.1	0.6 ± 0	0.9 ± 0.1
27	2	4.3 ± 0.6	1.9 ± 0.3	2.7 ± 0.5	5.0 ± 3.0	2.3 ± 0.3	1.0 ± 0.1	9.3 ± 2.8	1.6 ± 0.1	1.4 ± 1.3	0.8 ± 0
28	16	5.0 ± 0.9	2.1 ± 0.3	3.1 ± 0.6	8.0 ± 1.2	2.8 ± 0.6	1.1 ± 0.1	13.0 ± 2.0	1.7 ± 0.1	0.6 ± 0.1	0.8 ± 0.1
29	3	6.5 ± 0.2	3.0 ± 0.2	4.0 ± 0.2	10.3 ± 0.3	3.7 ± 0.2	1.3 ± 0.1	16.9 ± 0.3	1.6 ± 0	0.6 ± 0	0.8 ± 0.1
31	6	8.8 ± 1.0	3.7 ± 0.7	5.3 ± 0.7	14.9 ± 2.0	4.9 ± 0.8	1.9 ± 0.3	23.7 ± 2.9	1.6 ± 0.1	0.6 ± 0	0.8 ± 0.1
32	4	8.9 ± 0.8	3.7 ± 0.1	5.3 ± 0.2	14.3 ± 0.8	4.7 ± 0.3	2.0 ± 0.1	23.2 ± 1.6	1.7 ± 0.1	0.6 ± 0	0.8 ± 0
33	2	9.2 ± 0.1	3.9 ± 0.1	5.5 ± 0.1	15.7 ± 0.6	4.7 ± 0	2.1 ± 0.1	24.8 ± 0.5	1.7 ± 0	0.6 ± 0	0.8 ± 0
34	3	9.2 ± 0.5	3.8 ± 0.3	5.7 ± 0.3	14.7 ± 0.9	4.7 ± 0.7	2.1 ± 0.1	23.9 ± 0.7	1.6 ± 0	0.6 ± 0.1	0.8 ± 0.1
35	1	9.3	4.1	5.4	15.0	4.9	2.9	24.3	1.7	0.6	0.8
36	6	9.9 ± 0.4	4.0 ± 0.3	5.8 ± 0.4	16.7 ± 1.1	5.1 ± 0.4	2.2 ± 0.2	26.6 ± 1.5	1.7 ± 0.1	0.6 ± 0	0.8 ± 0.1
37	7	10.1 ± 0.5	4.3 ± 0.3	6.2 ± 0.3	17.2 ± 1.7	4.9 ± 0.5	2.2 ± 0.2	27.2 ± 2.1	1.6 ± 0.1	0.6 ± 0	0.9 ± 0.1
38	1	11.0	4.9	6.3	17.0	5.2	2.2	28.0	1.7	0.6	0.9

forest ponds. These sites comprised several hundreds to thousand eggs, spread between leaf litter, restricted to a few square meters at the very border of the ponds. All five ponds were dried up at that time. Egg size was between 3.5 and 6 mm. At all but one site, all eggs were of the same stage. Four of the five ponds remained water filled only in the high rainy season between August and November (Rödel, unpubl.). All spawning sites were located such that eggs only came in contact to open water after the ponds reached their maximum possible water capacity.

We assume that the eggs (4-5 mm) we discovered at site 1 were deposited on or shortly after September 8th. On September 16th, we flooded 100 eggs of these eggs with water. At that time the original pond was also water-filled. Within 5 min, 95 tadpoles, stage 25, hatched. None of these tadpoles possessed external gills, but all still had large yolk sacks. However, they immediately started feeding on the provided fish food. The remaining five tadpoles were still alive but apparently not able to hatch. We regularly preserved tadpoles of this series (SMNS 9776.1-73). On September 25th, the tadpoles reached stages 37-38 and had a body length of 10-11 mm. At that time, *P. aequiplicata* tadpoles in the forest pond had nearly twice the size of the ad libitum fed captive ones, and were about to metamorphose. In nature, time from hatching to metamorphosis seemed to last about two weeks. We kept another 106 eggs of the same site until September 23rd. Development of these eggs continued until stage 28 (fig. 3). The diameter of the eggs increased slightly during development (tab. 4). After flooding the 106 eggs with water, 38 larvae (stage 28) hatched within 40 minutes. After 90 minutes, only six tadpoles remained within the jelly capsules, obviously not able to hatch. Hatching success therewith equalled those eggs that were flooded a week before. Presuming that these eggs were deposited the 8th or shortly after that date, they survived within eggs for two weeks.

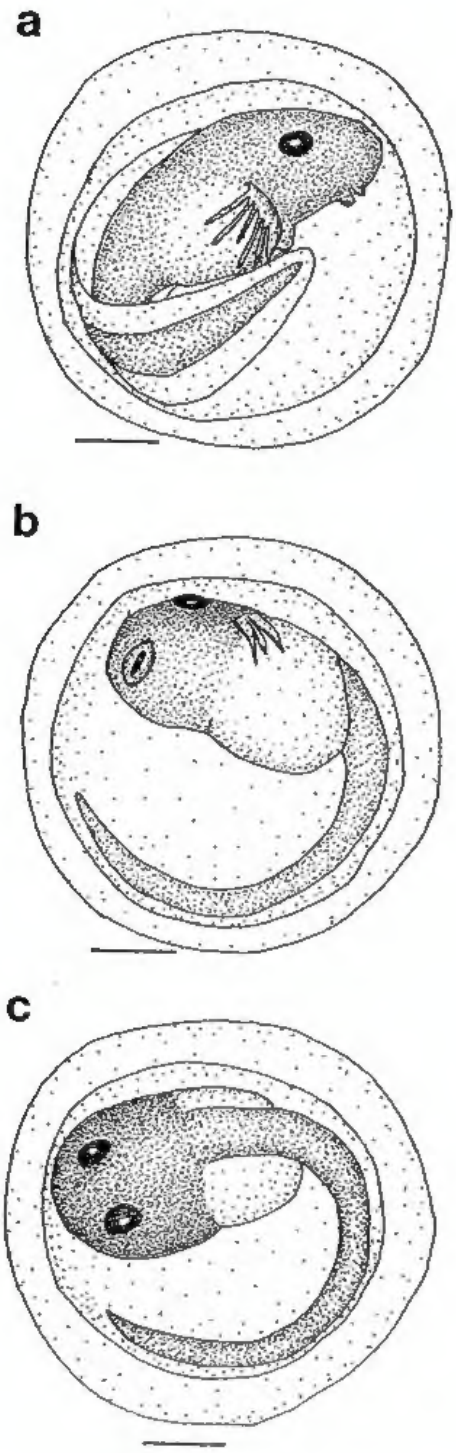

Fig. 3. – Lateral (a), ventral (b) and dorsal (c) view of egg stages of *Ptychadena aequiplicata*; (a) and (b) show individuals of stage 23, (c) figures a stage 25 tadpole. Scale bar: 1 mm.

Table 4. – Stage of pre-hatching *Ptychadena aequiplicata* and respective egg sizes.

Stage	*n*	Egg diameter	Stage	*n*	Egg diameter
20	2	4-4.7	24	2	4.8
21	8	4.2-5.1	25	2	5.5-5.7
22	3	4.4-5.1	27	2	5
23	2	5-5.3			

On September 18th, we collected much smaller eggs (3.5 mm) from a second site. We flooded 28 of these a day later. After 8 hours, only three tadpoles had hatched, all with external gills and large yolk sacks. After 24 hours, 13 tadpoles remained in the eggs, still alive. During the next 8 hours only four others managed to hatch.

We were able to monitor eggs at one site in the forest for one week. During that time it seemed that almost none of the eggs had disappeared, despite the fact that numerous ants, including driver ants (*Dorylus* sp.), were regularly encountered at that spot. We never detected any *P. aequiplicata* eggs that were covered with fungi.

Discussion

With the exception of its habitat preferences (e.g., Amiet, 1975; Largen & Dowsett-Lemaire, 1991), its voice (Schiøtz, 1964*b*; Amiet, 1974) and the size dimorphism in male and female *P. aequiplicata* (Perret, 1966), nearly nothing was known about the biology of this widespread West and Central African forest frog. *Ptychadena aequiplicata* tadpoles differ from other West African *Ptychadena* larvae by their bicoloured body, anterior part darker than posterior one. Other species have a more or less uniform beige or brown body (Lamotte & Zuber-Vogeli, 1953; Guibé & Lamotte, 1958; Lamotte et al., 1958, 1959; Lamotte & Perret, 1961; Rödel, 2000*a*). Another distinctive feature was the presence of three labial tooth rows in the upper lip in tadpoles more advanced than stage 28. Only a few individuals of *P. oxyrhynchus* and *P. mascareniensis* tadpoles are also known to possess three tooth rows in the upper lip (tab. 5).

While the free-swimming tadpoles fit the general characterisation of tadpoles of that genus (Altig & McDiarmid, 1999), being exotroph, lentic and benthic, clutch deposition clearly does not. All other known *Ptychadena* species deposit their eggs in a single layer as a surface film (Wager, 1986; Rödel, 2000*a*). *P. aequiplicata* deposit its eggs on the forest floor at the border of dried up forest ponds. These eggs are larger than other *Ptychadena* eggs (compare with Rödel, 2000*a*). Consequently, *P. aequiplicata* females seem to produce smaller clutches (tab. 6).

Our experiments showed that *P. aequiplicata* is very variable in respect to hatching time, lasting from a few days to more than two weeks. This strategy is very similar to that of a

Table 5. – Labial tooth row formulae (LTRF) of *Ptychadena* tadpoles.

LTRF	*Ptychadena* species (source)
1/1+1:1	*schubotzi* (RÖDEL, 2000*a*)
1/2	*schubotzi* (RÖDEL, 2000*a*); *bibroni* (GUIBÉ & LAMOTTE, 1958; LAMOTTE & PERRET, 1961); *submascareniensis* (LAMOTTE et al., 1958); *trinodis* (LAMOTTE et al., 1958); *tournieri* (LAMOTTE et al , 1958; RÖDEL, 2000*a*)
1/2+2	*schubotzi* (RÖDEL, 2000*a*)
1:1+1/1	*bibroni* (RÖDEL, 2000*a*); *submascareniensis* (LAMOTTE et al., 1958)
1:1+1/2	*pumilio* (LAMOTTE et al., 1959); *longirostris* (RÖDEL, 2000*a*); *oxyrhynchus* (GUIBÉ & LAMOTTE, 1958; WAGER, 1986, LAMBIRIS, 1988; RÖDEL, 2000*a*); *trinodis* (LAMOTTE et al., 1958; RÖDEL, 2000*a*); *mascareniensis* (PERRET, 1966)
2/2	*oxyrhynchus* (LAMBIRIS, 1988, 1989)
1:1+1/3	*oxyrhynchus* (LAMOTTE & ZUBER-VOGELI, 1953)
1:2+2/2	*oxyrhynchus* (GUIBÉ & LAMOTTE, 1958); *mascareniensis* (PERRET, 1966)

Table 6. – Egg numbers of West African *Ptychadena* species.

Species	Egg numbers	Source
P. aequiplicata	457-478	This paper
P. bibroni	800-1500	RÖDEL, 2000*a*
P. bibroni	1333 ± 643	BARBAULT & TREFAUT RODRIGUEZ, 1978; BARBAULT, 1984
P. schubotzi	500-1000	RÖDEL, 2000*a*
P. schubotzi	2011 ± 851	BARBAULT, 1984
P. oxyrhynchus	3476 ± 1542	BARBAULT & TREFAUT RODRIGUEZ, 1978, BARBAULT, 1984
P. mascareniensis	1079	BARBAULT, 1984

savannah frog, *Hemisus marmoratus*, who has to cope with rather unpredictable environmental conditions (RODEL et al., 1995, KAMINSKY et al., 1999). Forest ponds in TNP dry up surprisingly often, even during the rainy season (Rodel, unpubl. data) This high desiccation risk is due to the sandy soil in most parts of the forest. A variable time until hatching, in combination with the selection of spawning sites that assure that eggs or tadpoles come only into contact with water after ponds have completely filled, presumably offers tadpoles enough time to finish metamorphosis. When development continues within the eggs, tadpoles may additionally profit in competition with other tadpoles by their head start and towards smaller predators by their increased size (compare with RODEL, 1998)

According to STEWART (1967), another larger African ranid, *Rana fasciata fuelleborni*, deposits its eggs terrestrially Single eggs or small groups are attached underneath overhang-

ing mats of sedges, other dense vegetation or on moist earth about 2 5 cm above water. Hatched tadpoles drop into water. A large number of West African forest frogs also deposit their eggs outside of water, e.g various *Hyperolius* sp., all *Afrixalus* sp., *Chiromantis rufescens* and all *Leptopelis* sp. (SCHIØTZ, 1999; own data). In *Hyperolius*, *Afrixalus* and *Chiromantis*, tadpoles are often washed into the ponds even after small rains that might not provide sufficient water to assure metamorphosis. Depositing clutches terrestrially at the border of potential ponds might minimize the risk of hatching too early. However, at these sites predation risk might be higher than in arboreal clutches that are often protected by plant parts (*Afrixalus*) or foam (*Chiromantis*; but compare with RÖDEL et al., in press *b*). In contrast to this assumption we never observed that *P. aequiplicata* eggs were eaten, even when driver ants were present, nor did we ever observe eggs covered with fungi It might therefore be interesting to assay the egg capsules with respect to their chemical components.

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